OBSERVATIONS ON THE NESTING BIOLOGY OF *MELISSODES PERSIMILIS* CKLL. (HYMENOPTERA: ANTHOPHORIDAE)

Stephen L. Buchmann¹
Department of Entomology, University of California
Davis 95616

AND

C. Eugene Jones

Department of Biological Science, California State University, Fullerton 92634

Melissodes is the largest genus of Eucerini in the Western Hemisphere, with about 122 species (LaBerge, 1956a, 1956b, 1957, 1961, 1963). In his extensive studies of this group LaBerge described the nesting biology and floral visitation records for many species. Observations on the sleeping habits of male Melissodes have been made by Banks (1902) on M. bimaculata (Lepeletier); Mathewson and Daly (1955) on M. perplexa Cresson; Evans and Linsley (1960) on M. paroselae Cockerell and M. spp. near confusa Cresson; Linsley (1962) on M. paroselae and M. tristis Cockrell; LaBerge (1961) on M. confusa Cresson; Chemsak and Thorp (1962) on M. robustion Cockerell; Thorp and Chemsak (1964) on M. pallidisignata; Clement (1973) on M. rustica (Say). Descriptions of the nesting biology and larval morphology of Melissodes are still quite fragmentary. Melissodes composita (Hurd and Linsley, 1959), M. pallidisignata (Thorp and Chemsak, 1964) and M. rustica (Clement, 1973) have been best studied. Additional data on nesting biology are presented by Ashmead (1894) for M. bimaculata; Graenicher (1905) for M. trinodis Robertson; Rau (1922) for M. agilis Cresson; Hicks (1926) for M. mizeae Cockerell and M. subagilis (Cockerell); Custer (1928, 1929) for M. obliqua Say; Scullen (1928) for M. mysops Cockerell; Hicks (1936) for M. timberlakei Cockerell; Linsley (1946) for M. timberlakei; Janvier (1955) for M. sexcincta (Lepeletier); Linsley, MacSwain and Smith (1955) and MacSwain (1958) for M. robustior; Michener and Lange (1958) for M. nigroaenea (Smith); Hurd and Linsley (1959) for M. composita Tucker; Thorp and Chemsak (1964) for M. pallidisignata; and Clement (1973) for M. rustica (Say). Descriptions and figures of mature larvae of Melissodes have been provided by Michener (1953), Rozen (1965) and by Clement (1973). Clement (1973) provides the most recent information on the genus. Melissodes persimilis is known from Guatemala, Honduras and Panama. It is related to the northern species M. montana and M. confusa (LaBerge, 1956a, 1956b, 1957; Michener, 1944). It is a moderate-sized bee, the females average approximately 12 mm in length and the males ranging from 9–12 mm long. This species is sexually dimorphic in that the slender males are smaller with longer antennae, while the females are more robust and darker in color. Body color varies from an ochraceous to dull ferrugineous brown.

Our studies included preliminary observations on the nesting biology of M. persimilis and augment the existing somewhat fragmentary nesting and life history data for this genus.

Nesting Biology

A small nesting site (less than 4 m²) of *Melissodes* (*Eumelissodes*) persimilis Ckll. was discovered on January 31, 1972. It contained about one hundred active burrows. The site was located about one-half kilometer behind the Organization for Tropical Studies, Finca Las Cruces field station (now the Las Cruces Tropical Botanic Garden) at San Vito de Java, Puntarenas Province, Costa Rica. This area is at an elevation of approximately 1400 meters and has been described as a premontane wet forest by Holdridge (1967). The bees were tunneling into a widened portion of the main trail in loosely compacted, light-colored, sandy soil, devoid of vegetation except some grasses along the edges. To both sides of the trail (about 5 meters on both sides and adjacent to the site) some secondary growth occurred in front of the lush vegetation of the wet forest. We studied these bees on January 31 and February 1.

Female *Melissodes* visited flowers (a number of unidentified composites, Asteraceae, growing near the aggregative nest site) for pollen. An analysis of the pollen loads from several bees indicated a high percentage of composite pollen suggesting that *M. persimilis* is oligolectic on composites. Primary nectar sources for males or females were not discovered.

During both days of observation, warm temperatures were prevalent and bees were observed flying over the site by 0900 EST. Male bees were the first to fly in the morning. By 0900, hundreds of males were seen flying very low (@ 3 cm) over the site. They flew very rapidly in erratic flight paths, occasionally alighting, entering a burrow momentarily, or attempting copulation with a female. The ratio of visible males to females was about 10 or 15 males to every female. Some samples were taken by rapidly sweeping over the nests with an aerial insect net. Every observed mating took place at the nesting site and males did not patrol the flowers that were visited by conspecific females. Males patrolling the nesting aggregation attempted to copulate with emerging females as well as those returning from foraging "bouts." Returning pollen-laden females were apparently unreceptive to-

ward persistent male attacks. Pairs of bees dropped to the ground near burrow entrances where "courtship" movements and copulation (movements and intromission) ensued. The duration of copulation activity was approximately one minute in several timed cases. Additional patrolling males often attempted to interfere with paired or copulating bees. Often there were as many as six males engaged in this activity (attempted displacement of the primary male), and the groups of bees moved as a writhing ball across the forest trail. Females that were provisioning their cells often repulsed males. It was not determined whether a single female provisioned more than one nest during her lifetime. Although the nests were grouped into a tight aggregation, there appeared to be no cooperation among neighboring females in nest construction.

Females spent the night singly in their nests and males spent the night singly or communally in other old, or possibly new burrows.

Females used their mandibles and forelegs to excavate the burrows. Sand loosened while digging was propelled out of the tunnel with the posterior legs, as the bees backed out of their burrows. Loose sand was deposited in a circular tumulus about the opening (Fig. 1). The entrance is loosely plugged with sand through which the female passes each time she enters the nest. The burrow was filled all the way down with loose fill soil upon completion of the provisioning by the female. Bees were observed provisioning cells with two types of composite pollen. The most common was a deep yellow-orange, whereas the other was a lighter yellow. Female bees emerging from their burrows following a provisioning trip always paused briefly at the entrance of their nests before taking flight for the next trip. This behavior was described by Clement (1973) who considered it to be a response to avoid attracting parasitic bees and other insects to the vicinity of the burrow. No evidence of parasitism from other bees was observed while watching the activity in the nesting area and no parasitic bee larvae were excavated from Melissodes cells. However, a small red mutillid female entered one burrow. The wasp remained in the burrow for 30 seconds and came up with her head lightly dusted with pollen.

The burrow averages 5–6 mm in diameter and culminates in a single cell 8 to 12 cm below the surface of the soil (Fig. 1). The burrows went straight down and angled only a centimeter or less above the cell (Fig. 1A). The cell was straight sided and symmetrical with a concave bottom. The maximum internal cell diameter was 8 mm. The curved egg ranged from 2.5 to 3 mm long (N=3) and was attached by one end (probably its posterior) to the center of a pollen ball with a slightly concave upper surface. The egg was dull white in color, not shiny. This surface was moist and glistened as if the female bee had applied a light layer of nectar to the surface of the pollen mass. The cells were not rigid, crumbled easily, and could not be excavated intact. The orientation of the cells was angular with respect to the soil

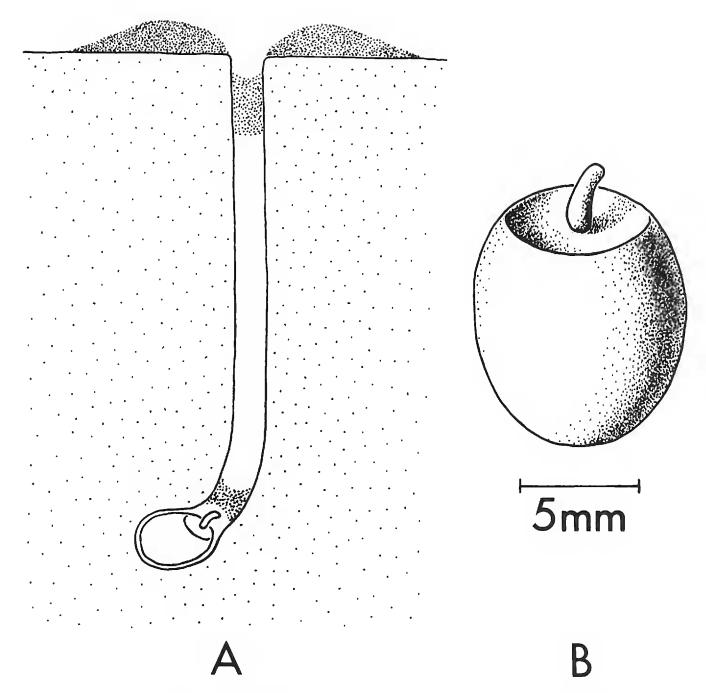


Fig. 1. Nest architecture of *Melissodes persimilis* Ckll. A. Complete nest showing radial tumulus, opening plug and cap over the provisioned cell. B. Pollen ball showing the apical attachment of the egg by one end to the concave surface of the pollen mass.

surface, and this angle was somewhat variable. The cell linings were smooth but not shiny and were not lined with wax or other adult secretions. No information was obtained on cell closure although it may have been a concave spiral as viewed from inside, as described for other eucerines (Rozen, 1964, 1969, 1974). The provisions (pollen ball) occupied the entire rear portion of the cell with no space between the pollen and the cell walls. The surface of the provisions were slightly concave near the point of egg attachment. There was no apparent odor or swelling of provisions to indicate the active fermentation of the brood provisions. Eggs, young instars and pre-

defecating larvae were present at the same time in the site. No data were gathered on pupal morphology or cocoon construction because these stages were not present during our observations.

Several pre-defecating larvae were collected and preserved. These were critically examined and found to differ insignificantly from those *Melissodes* species illustrated by previous workers (Michener, 1953; Rozen, 1965; Clement, 1973). Representative larvae are now on deposit in the larval bee collection under the care of Jerome G. Rozen (American Museum of Natural History).

Discussion

Our study of *M. persimilis* has revealed both similarities and differences with *M.* (*Eumelissodes*) pallidisignata and *M. rustica* (Thorp and Chemsak, 1964; Clement, 1973).

In all these species, digging behavior is very similar and a loose plug of sand forms a burrow plug through which the female must pass each time she enters or leaves the nest. This appears to be an adaptation to prevent parasitic bees and other insects from entering or easily locating the burrow (Clement, 1973). In *M. pallidisignata*, like *M. persimilis*, the burrow contains an arch-like section near the end of the tunnel that prevents the sand plug from entering the cell while it is being provisioned. This apparently serves the same function as does the short horizontal section of *M. rustica* burrows (Clement, 1973). Nests of both *M. rustica* and *M. persimilis* seem to be more architecturally uniform than do those of *M. pallidisignata*. In all three species only one cell per burrow is constructed. All three are solitary bees which nest in at least fairly large and dense aggregations.

There are also differences in the ethology of the three species. Males of *M. pallidisignata* either spend the night on floral disks or more often in the loose plug of active burrows (Thorp and Chemsak, 1964). Males of *M. rustica* apparently spend their nights in old burrows or nearby crevices in volcanic rocks (Clement, 1973) and males of *M. persimilis* "sleep" in old and possibly new burrows. In pollen masses collected by females of *M. persimilis* there was no evident fermenting odor as was reported in the other two taxa. It has also been suggested by Thorp and Chemsak (1964) that the liquification of the surface layer of the pollen mass was due to larval secretions by early instars, as they were unable to find it on pollen masses with eggs alone. Clement (1973) agreed with these findings and reported a similar condition in the pollen mass of *M. rustica*. Our findings for *M. persimilis* suggest an alternative because the liquid layer was present with both eggs and early instar larvae, this layer may be the final addition of liquic nectar left by the provisioning female bee.

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Literature Cited

- Ashmead, W. H. 1894. The habits of the aculeate Hymenoptera I. Psyche, 7:19–26.
- Banks, N. 1902. Sleeping habits of certain Hymenoptera. J. New York Entomol. Soc., 10:209–214.
- Chemsak, J. A., and R. W. Thorp. 1962. Note on the sleeping habits of males of *Melissodes robustior* Cockerell (Hymenoptera: Apoidea). Pan-Pac. Entomol., 38:53-55.
- Clement, S. L. 1973. The nesting biology of *Melissodes* (*Eumelissodes*) rustica (Say), with a description of the larva (Hymenoptera: Anthophoridae). J. Kans. Entomol. Soc., 46:516-525.
- Custer, C. P. 1928. On the nesting habits of *Melissodes* Latr. Can. Entomol., 60:28–31.
- Custer, C. P. 1929. Notes on cocoons and parasites of *Melissodes obliqua* and nests of *Perdita opuntiae*. Psyche, 36:293–295.
- Evans, H. E., and E. G. Linsley. 1960. Notes on sleeping aggregation of solitary bees and wasps. Bull. So. Calif. Acad. Sci., 59:30-37.
- Graenicher, S. 1905. Some observations on the life history and habits of parasitic bees. Bull. Wisc. Nat. Hist. Soc., 3:153–167.
- Hicks, C. H. 1926. Nesting habits and parasites of certain bees of Boulder County, Colorado. Univ. Colo. Studies. Sept. 1926, 217–252 pp.
- Hicks, C. H. 1936. Nesting habits of certain western bees. Can. Entomol., 68:47-52.
- Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica, Revised ed.
- Hurd, P. D., and E. G. Linsley. 1959. Observations on the nest-site behavior of *Melissodes composita* Tucker and its parasites, with notes on the communal uses of nest entrances (Hymenoptera: Apoidea). Entomol. News, 70:141-146.
- Janvier, H. 1955. Les nid et la nidifications chez quelques abeilles des Andes tropicales. Ann. Sci. Nat. Zool., 17:311–349.
- LaBerge, W. E. 1956a. A revision of the bees of the genus *Melissodes* in the North and Central America. Part I. Univ. Kans. Sci. Bull., 37:911–1194.
- LaBerge, W. E. 1956b. Ibid. Part II, 38:533-578.
- LaBerge, W. E. 1957. The genera of the bees of the tribe Eucerini in North and Central America. Amer. Mus. Nov., 1837:1–44.
- LaBerge, W. E. 1961. A revision of the bees of the genus *Melissodes* in North and Central America. Part III. Univ. Kans. Sci. Bull., 42:283-663.

- LaBerge, W. E. 1963. New species and records of little-known species of *Melissodes* from North America. Univ. Nebr. St. Mus. Bull., 4:227–242.
- Linsley, E. G. 1946. Insect pollinators of alfalfa in California. J. Econ. Entomol., 39:18-29.
- Linsley, E. G. 1962. Sleeping aggregations of aculeate Hymenoptera—II. Ann. Entomol. Soc. Amer., 55:148–164.
- Linsley, E. G., J. W. MacSwain, and R. F. Smith. 1955. Biological observations on *Xeno-glossa fulva* Smith with some generalizations on biological characters of other eucerine bees. Bull. So. Calif. Acad. Sci., 54:128–141.
- MacSwain, J. W. 1958. Longevity of some anthophorid bee larvae (Hymenoptera: Apoidea). Pan-Pac. Entomol., 34:40.
- Mathewson, J. A., and H. V. Daly. 1955. A brief note on the sleep of male *Melissodes* (Hymenoptera: Apidae). J. Kans. Entomol. Soc., 28:120.
- Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist., 82:151–326.
- Michener, C. D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. Univ. Kans. Sci. Bull., 35:987–1102.
- Michener, C. D., and R. B. Lange. 1958. Observations on the ethology of Neotropical anthophorine bees (Hymenoptera: Apoidea). Univ. Kans. Sci. Bull., 39:69–96.
- Rau, P. 1922. Ecological and behavior notes on Missouri insects. Trans. Acad. Sci., St. Louis, 24:1-71.
- Rozen, J. G. 1964. The biology of *Svastra obliqua obliqua* (Say), with a taxonomic description of its larvae (Apoidea, Anthophoridae). Amer. Mus. Novitates, 2170:1–13.
- Rozen, J. G. 1965. The larvae of the Anthophoridae (Hymenoptera: Apoidea) Part I. Introduction, Eucerini, and Centridini (Anthophorinae). Amer. Mus. Nov., 2233:1–27.
- Rozen, J. G. 1969. Biological notes on the bee *Tetralonia minuta* and its cleptoparasite, *Morgania histrio transvaalensis* (Hymenoptera: Anthophoridae). Proc. Ent. Soc. Washington, 71:102–107.
- Rozen, J. G. 1974. Nest biology of the eucerine bee *Thygater analis* (Hymenoptera: Anthophoridae). Jour. New York Ent. Soc., 82:230–234.
- Scullen, H. A. 1928. *Melissodes mysops* Cockerell nesting in Oregon (Anthophoridae: Hymenoptera). Pan-Pac. Entomol., 4:176.
- Thorp, R. W., and J. A. Chemsak. 1964. Biological observations on *Melissodes (Eumelissodes) pallidisignata*. Pan-Pac. Entomol., 40:75–83.

Footnote

¹ Present address: USDA-SEA-AR-WR, Carl Hayden Bee Research Center, 2000 East Allen Road, Tucson, Arizona 85719.